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# Managing the Risk of European Corn Borer Resistance to Transgenic Corn: An Assessment of Refuge Recommendations

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# Managing the Risk of European Corn Borer Resistance to Transgenic Corn: An Assessment of Refuge Recommendations

## **Abstract**

The use of Genetically Modified Organisms (GMOs) in agriculture has been on the rise since 1995. Scientists have been working to develop a high-dose refuge management plan that can effectively delay European corn borer resistance to pesticidal GMO corn. This paper develops a stochastic agricultural production model to assess and provide insight into the reasons why refuge recommendations remain controversial.

## **Keywords**

Agriculture, Risk management, Entomology

## **Disciplines**

Agricultural Science | Agriculture | Agronomy and Crop Sciences | Entomology

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# **Managing the Risk of European Corn Borer Resistance to Transgenic Corn: An Assessment of Refuge Recommendations**

Terrance M. Hurley, Silvia Secchi, Bruce A. Babcock, and Rick Hellmich

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## **ABSTRACT**

Industry and scientists have worked to develop a high-dose refuge management plan that can effectively delay European corn borer (ECB) resistance to new genetically modified pesticidal corn. For a high dose, the corn expresses enough pesticide to kill all but the most resistant corn borers. For refuge, producers plant a traditional corn variety that allows susceptible corn borers to thrive and mate with resistant corn borers, slowing the proliferation of resistance. In general, the more refuge that is planted the less likely resistance. While there is general agreement on the basic premise of the high-dose refuge plan, how much refuge is needed to manage resistance is still being debated. This paper develops a stochastic agricultural production model to assess and provide insight into the reasons why refuge recommendations remain controversial.

We find that (a) reducing the risk of resistance requires decreasing agricultural productivity, (b) new technologies that are currently being tested will reduce the risk of resistance, (c) producer noncompliance increases the risk of resistance, and (d) nonrandom mating in the ECB populations increases the risk of resistance. Disagreements over the importance of nonrandom mating and producer compliance can be resolved with additional research. Controversy will remain, however, as long as producers and industry continue to bear most of the financial cost of reducing the risk of resistance through higher refuge recommendations.

## **MANAGING THE RISK OF EUROPEAN CORN BORER RESISTANCE TO TRANSGENIC CORN: AN ASSESSMENT OF REFUGE RECOMMENDATIONS**

The use of Genetically Modified Organisms (GMOs) in agriculture has been on the rise since 1995. Although these transgenic organisms can embody either innovative product or process characteristics, to this day they have mainly offered new solutions to pest control. In terms of acreage planted, some of the most successful GMOs have been those genetically engineered to kill pests by expressing a protein that is found in the soil bacterium *Bacillus thuringiensis* (Bt).<sup>1</sup> The potential for pesticidal GMOs to increase agricultural productivity can not be denied; however, empirical evidence suggests these benefits could be diminished by the development of resistance to Bt (Hama et al. 1992; Tabashnik et al. 1992; Martinez-Ramirez et al. 1995; Tabashnik et al. 1995).

As with other highly selective pesticides, controlling pests using a GMO has two important dimensions. First, surviving pests propagate, making the pest population renewable (Regev et al. 1983). Second, pest susceptibility to GMO toxins is generally nonrenewable (Hueth and Regev 1974; Regev et al. 1976; Regev et al. 1983). The increased selection pressure placed on pests by a GMO favors the survival of resistant pests. As resistance develops, the GMO is increasingly less effective for pest control. Because insect pests are mobile, farmers may fail to account for the external benefits of pest suppression efforts and costs of resistance they impose on their neighbors.

Concerns about resistance prompted the U.S. Environmental Protection Agency (EPA) to conditionally register the first generation of pesticidal GMOs. The conditional registrations were designed to give industry enough time to develop and implement effective resistance management plans, while also collecting important information on the potential risk of resistance. To manage resistance, industry has focused on a high-dose refuge strategy. For a high dose, the GMO must express extremely high levels of toxin so that all but the most resistant pests survive. For refuge, farmers are expected to plant part of their crop acreage to a crop that does not use the GMOs toxins for pest control. Refuge allows susceptible pests to thrive so they can mate with resistant pests, reducing selection pressure and extending the efficacy of the GMO.

Evidence suggests that a high-dose refuge strategy can control resistance effectively in many circumstances provided an adequate amount of refuge is planted. How much refuge is adequate remains a question of debate because of important biological factors that are either random in nature or not precisely

known, and because of economic factors that both determine a stakeholder's willingness to accept greater risk and influence the effectiveness of the refuge.

The purpose of this paper is to develop a model to better understand and provide insight into the debate over refuge recommendations for Bt corn that is used to control the European corn borer in the central and western United States. Currently, recommendations range from 20 to 30 percent when refuge is not treated with pesticides and from 20 to 40 percent when treated with non-Bt pesticides. By exploring key issues of contention within a consistent analytic framework, we provide useful information that can help guide the policy debate over refuge recommendations. Additionally, a Bayesian method is developed that uses pest survival data from the field to quantify the risk of resistance. Incorporating a second gene, which allows us to evaluate the potential of GMOs that express multiple toxins, extends previous bioeconomic models of pest resistance. Pest suppression is explored using alternative stochastic pest population models, and producer compliance with recommendations is addressed using recent survey data.

Reviewing the debate over refuge recommendations, we have identified four sources of controversy: (a) the value of reducing the risk of resistance, (b) the potential introduction of new multiple toxin plants, (c) producer compliance, and (d) the degree of nonrandom mating. We find that producers and industry will generally prefer a lower refuge recommendation because they currently bear most of the financial cost of reducing the risk of resistance with higher refuge recommendations. Eventually, plants that express multiple toxins will be commercially available. These new plants will reduce the risk of resistance. Some members of industry support a lower recommendation because they believe these new technologies will soon reduce the need for resistance management. Entomologists and other scientists have supported a higher recommendation because they are less willing to rely on the introduction of these new technologies. Producer noncompliance with refuge recommendations may dictate either a higher or lower recommendation. If a producer's voluntary compliance decreases as the recommendation increases because of greater compliance cost, a higher refuge recommendation may be necessary to increase the actual size of refuge. However, if a higher recommendation results in lower compliance, an increase in the recommendation can be counterproductive. With the rate of noncompliance we explore, a higher recommendation is appropriate. Nonrandom mating reduces the effectiveness of refuge, resulting in the need for a higher recommendation. Currently, the degree of nonrandom mating is not known. Different assumptions regarding the degree of nonrandom mating have therefore resulted in different recommendations.



### The Conceptual Model

Optimally, refuge recommendations should adjust over time as pest susceptibility becomes increasingly scarce and as new information becomes available to resolve unanswered questions. Deriving an optimal exhaustion path *ex ante* is a daunting task because the optimal path is conditioned on what new information arises in the future. The types of new information that can arise include the realization of unpredictable events such as the level of pest pressure in a particular season, new experimental or field data that elucidates unknown factors such as the current level of resistance to Bt, and the realization of unforeseen events such as the discovery of substitute or complementary technologies. Alternatively, imposing an inflexible, safe minimal recommendation based on the best available information is a more manageable task, though not optimal because it does not incorporate new information as it becomes available or address the increasing scarcity of pest susceptibility.

The impracticality of designing temporally optimal refuge recommendations and the inflexibility and suboptimality of a temporally inflexible safe minimal recommendation have resulted in the adoption of an adaptive strategy. The adaptive strategy sets a safe minimal recommendation to satisfy a specific set of objectives, but revises this recommendation as available information warrants. Currently, two objectives that have been identified are (1) the preservation of pest susceptibility and (2) the maintenance of the agricultural benefits provided by Bt corn. Specifically, the International Life Sciences and Health and Environmental Sciences Institutes (ILSI-HESI) in a recent report explicitly defined the preservation of pest susceptibility as the maintenance of resistant allele frequencies below 0.50 for 30 generations. Unfortunately, less specificity has been given to objective (2).

The model we develop builds on Hurley et al. (1997) by incorporating important sources of uncertainty related to the current level of resistance, the survival rate of resistant pests, and European corn borer (ECB) population dynamics. Focusing on a simplified production region with a single crop (corn) and pest (ECB) concisely illustrates important issues that influence refuge recommendations.<sup>2</sup> The scope of the region we consider is defined by pest mobility where we assume migration is negligible.<sup>3</sup> There are two varieties of corn planted in the region: a Bt corn event, denoted by *Bt*, and a non-Bt isolate that is used as refuge, denoted by *Non*.<sup>4</sup> Define  $N$  as the proportion of the refuge recommended, while  $N_t^e$  and  $1 - N_t^e$  is the effective proportion of refuge and Bt corn planted in season  $t$ . The effective proportion of refuge planted can depend on the refuge recommendation, pest pressure, voluntary compliance rates, and Bt corn adoption rates, for instance.

## Genetic Variation

Current Bt events utilize one of three toxins (Cry I(A)b, Cry I(A)c, or the more recently registered Cry 9c), but in the future new events may express multiple toxins. To be able to explore the resistance management benefits of multiple toxins, we use a genetic model with two genes (Hartl 1988) that are denoted by  $a$  and  $b$ . A gene consists of two alleles, one contributed by the mother and the other one by the father. We assume there are only two types of alleles for each gene, one conferring resistance,  $R^a$  and  $R^b$ , with all others conferring susceptibility,  $S^a$  and  $S^b$ . A gamete is a combination of alleles, one for each gene, passed to an offspring by the mother or father. With our two-gene model there are four distinct types of gametes that a parent can pass to its offspring: resistant alleles for both genes,  $R^a/R^b$ ; susceptible alleles for both genes,  $S^a/S^b$ ; or one of two combinations of resistant and susceptible alleles,  $R^a/S^b$  or  $S^a/R^b$  such that  $(\in \{R^a/R^b, R^a/S^b, S^a/R^b, S^a/S^b\})$ . Combining the gametes from the mother and father,  $(\times)$ , produces the 16 possible allelic combinations illustrated in Table 1. For the  $v$ th gene,  $v \in \{a, b\}$ , the offspring can be either a resistant homozygote,  $R^v R^v$ ; a susceptible homozygote,  $S^v S^v$ ; or a heterozygote,  $R^v S^v$  or  $S^v R^v$ . Therefore, although there are 16 different allelic combinations, some are redundant, resulting in nine distinct genetic combinations that may differ in terms of their survival on Bt corn and refuge.

Table 1: Punnett square of allelic types

Father's Contribution	Gamete types	Mother's Contribution			
		$R^a/R^b$	$R^a/S^b$	$S^a/R^b$	$S^a/S^b$
	$R^a/R^b$	$R^a R^a / R^b R^b$	$R^a R^a / S^b R^b$	$S^a R^a / R^b R^b$	$S^a R^a / S^b R^b$
	$R^a/S^b$	$R^a R^a / R^b S^b$	$R^a R^a / S^b S^b$	$S^a R^a / R^b S^b$	$S^a R^a / S^b S^b$
	$S^a/R^b$	$R^a S^a / R^b R^b$	$R^a S^a / R^b S^b$	$S^a S^a / R^b R^b$	$S^a S^a / R^b S^b$
	$S^a/S^b$	$R^a S^a / R^b S^b$	$R^a S^a / S^b S^b$	$S^a S^a / R^b S^b$	$S^a S^a / S^b S^b$

## Biological Dynamics

Midwestern ECB populations are normally bivoltine (i.e., produce two generations per season). The level of ECB pressure experienced in a region varies dramatically depending on pest pressure in the previous generation and other random climatic and environmental factors (Royama 1992). Define  $N_{t,g}$  as the average number of ECB per plant emerging at the beginning of a generation, while  $N_{t,g}^S$  is the average number of ECB per plant surviving to damage crops and reproduce in season  $t$  and generation  $g$ .

$$(1) \quad N_{t+1,1} \sim N_1(N_{t,2}^S) \text{ and}$$

$$(2) \quad N_{t2} \sim N_1(N_{t1}^S).$$

Let Equations (1) and (2) state that the ECB population emerging at the beginning of season  $t$  and generation  $g$  is randomly distributed conditional on the previous generation's surviving population. They also assume that reproductive rates are not influenced directly by genetic variation and that the effect of the previous generation on the first generation of ECB may differ from the effect of the second generation on the first, usually due to the overwintering.

While reproductive rates are not influenced directly by genetic variation, the size of the surviving pest population is influenced. In particular, the surviving pest population will depend on the emerging pest population, genetic variation, the effective proportion of refuge, and genetic survival rates on Bt corn and refuge that are related to overall fitness and susceptibility to Bt. Define  $\mathfrak{A}_{t g j}$  as the proportion of the  $j$ th gamete in season  $t$  and generation  $g$  where  $\mathfrak{A}_{t g j} \in [0.0, 1.0]$  for  $j \in \gamma$ ,  $\sum_{j \in \gamma} \mathfrak{A}_{t g j} = 1.0$ , and  $\mathfrak{A}_{t g}$  as the vector of these proportions that is currently not precisely known. Define  $\Delta_g^{Bt}$  and  $\Delta_g^{Non}$  as vectors of survival rates on Bt corn and refuge for the nine distinct genetic combinations in generation  $g$ . As with current levels of resistance, these survival rates are not precisely known. Surviving pests on the  $i$ th crop,  $i \in \{Bt, Non\}$ , can now be written as the average survival rate of pests, which is a function of gamete frequencies and survival rates, multiplied by the emerging pest population:

$$(3) \quad N_{t1}^i = \rho(\mathfrak{A}_{t1}, \Delta_1^i) N_{t1} \text{ and}$$

$$(4) \quad N_{t2}^i = \rho(\mathfrak{A}_{t2}, \Delta_2^i) N_{t2}.$$

All else equal, the surviving population tends to increase as the proportion of gametes with resistant alleles increases, survival rates increase, and the emerging pest population increases. The average number of surviving pests is then an average of pests on Bt corn and refuge weighted by the effective size of the refuge:

$$(5) \quad N_{t1}^S = N_t^e N_{t1}^{Non} + (1 - N_t^e) N_{t1}^{Bt}, \text{ and}$$

$$(6) \quad N_{t2}^S = N_t^e N_{t2}^{Non} + (1 - N_t^e) N_{t2}^{Bt}.$$

Finally, the proportion of gametes containing resistant alleles evolves depending on previous levels of resistance, survival rates, and the degree of selection imposed by the effective size of the refuge:

$$(7) \quad \Gamma_{t1} = \Gamma(\Gamma_{t-12}, \Delta_2^{Bt}, \Delta_2^{Non}, N_{t-1}^e), \text{ and}$$

$$(8) \quad \Gamma_{t2} = \Gamma(\Gamma_{t1}, \Delta_1^{Bt}, \Delta_1^{Non}, N_t^e).$$

All else equal, resistance tends to increase as the survival rate of genetic combinations with susceptible alleles decreases and as the effective size of the refuge declines.

### Biological Objectives

The primary biological objective that has been specified for choosing the refuge recommendation is to prolong the efficacy of Bt corn by preserving pest susceptibility over the length of a planning horizon,  $T$ . To formalize this objective, we first must specify what preserving pest susceptibility means. The ILSI-HESI report defines preserving pest susceptibility as not allowing resistant gametes to exceed an acceptable threshold. Since resistance is generally treated as irreversible within a reasonable period of time, this objective implies that resistance should not exceed an acceptable level at  $T$ . For events expressing a single toxin, the definition of a resistant gamete is straightforward. The appropriate definition of a resistant gamete when events express multiple toxins is more complicated. Since the current level of resistant gametes and survival rates is not precisely known, this definition can only be satisfied in a probabilistic sense; therefore, an acceptable rate of error in meeting this objective must also be specified. An explicit biological objective can be formalized by defining three constraints that must be satisfied by the refuge recommendation:

$$(9) \quad \Psi^a(\phi, \theta^a) = \Pr\left(\Gamma_{T2}^{R^a|R^b} + \Gamma_{T2}^{R^a|S^b} \leq \theta^a\right) \leq 1 - \Psi$$

$$(10) \quad \Psi^b(\phi, \theta^b) = \Pr\left(\Gamma_{T2}^{R^a|R^b} + \Gamma_{T2}^{S^a|R^b} \leq \theta^b\right) \leq 1 - \Psi, \text{ and}$$

$$(11) \quad \Psi^{ab}(\phi, \theta^{ab}) = \Pr\left(\Gamma_{T2}^{R^a|R^b} \leq \theta^{ab}\right) \leq 1 - \Psi$$

where  $\theta^a$ ,  $\theta^b$ , and  $\theta^{ab}$  are the maximum acceptable proportion of resistant alleles at the beginning of  $T$  for gene  $a$ , gene  $b$ , and both genes concurrently; and  $\Psi$  is the maximum acceptable rate of error.

If an event expresses a single toxin that selects for resistance only at gene  $a$ , for example, we can focus on resistance at gene  $a$  by setting  $\theta^a = \theta^{ab} \in (0.0, 1.0)$  and  $\theta^b = 1.0$ . For events that express two toxins, the appropriate set of objectives may be (1)  $\theta^a \in (0.0, 1.0)$ ,  $\theta^b \in (0.0, 1.0)$ , and  $\theta^{ab} = \text{Min}\{\theta^a, \theta^b\}$

or (2)  $\theta^{ab} \in (0.0, 1.0)$  and  $\theta^a = \theta^b = 1.0$ . For (1), the constraints imply that the objective is to preserve susceptibility for both genes independently, which might be reasonable if multiple toxin events do not completely replace single toxin events. For (2), the constraints imply an objective of preserving pest susceptibility only for multiple toxin events. Currently, whether (1) or (2) should be used to evaluate multiple toxin events has not been addressed explicitly.

### Agricultural Benefits

The second objective that has been identified for refuge recommendations is the preservation of the agricultural benefits of Bt corn. While an explicit definition of the agricultural benefits of Bt corn has not been articulated, we believe the spirit of this objective is captured by the expected net present value of agricultural production.

Assume the expected pest-free yield for both crops is  $Y$  bushels/acre, but that actual yields may vary due to pest pressure. Let  $D_t^i = d(N_{t1}^i, N_{t2}^i)$  be the average proportion of yield loss on the  $i$ th crop where  $D_t^i \in [0.0, 1.0]$  is strictly increasing in the number of pest per plant in both generations. The average yield per acre for the  $i$ th crop is  $Y_t^i = Y(1 - D_t^i)$  in season  $t$ . Let  $C^i$  be the average per acre cost of production for the  $i$ th crop. Finally, let  $P$  be the expected real price of corn and  $\delta$  be the discount rate. The expected net present value of agricultural production given random pest populations and uncertainty regarding current levels of resistance and survival rates is

$$(12) \quad ENPV(\phi) = E \left[ \sum_{t=0}^{T-1} \delta^t \left\{ \begin{aligned} &\phi_t^e \left[ PY(1 - D_t^{Non}) - C^{Non} \right] \\ &+ (1 - \phi_t^e) \left[ PY(1 - D_t^{Bt}) - C^{Bt} \right] \end{aligned} \right\} \right]$$

where  $E$  is the expectation operator defined over the joint distribution of current resistance frequencies, survival rates, and future pest pressure given the best available scientific information, and current pest pressure. Equation (12) uses the effective proportion of refuge to take a weighted average of the expected return per acre on refuge and Bt corn. This average return per acre is then discounted and summed over the length of the planning horizon.

Substituting Equations (1)-(8) into (12), we can derive the refuge recommendation that maximizes (12) subject to the biological objectives in Equations (9)-(11). The Lagrangian function can be written as:

$$\begin{aligned}
(13) \quad L = & ENPV(\phi) + \lambda^a \left( 1 - \Psi - \Psi^a(\phi, \theta^a) \right) \\
& + \lambda^b \left( 1 - \Psi - \Psi^b(\phi, \theta^b) \right) \\
& + \lambda^{ab} \left( 1 - \Psi - \Psi^{ab}(\phi, \theta^{ab}) \right) \\
& + \lambda^\phi (1 - \phi).
\end{aligned}$$

Assuming second-order sufficiency conditions are satisfied and the solution is interior, the first-order marginal condition is

$$(14) \quad \frac{\partial ENPV}{\partial \phi} = \lambda^a \frac{\partial \Psi^a}{\partial \phi} + \lambda^b \frac{\partial \Psi^b}{\partial \phi} + \lambda^{ab} \frac{\partial \Psi^{ab}}{\partial \phi}.$$

If the effective size of refuge is positively related to the refuge recommendation, Hurley et al. (1997) suggest the left-hand side of Equation (14) will initially be positive, as increasing refuge extends the efficacy of Bt corn and increases long-run profits. With enough refuge, Bt corn will remain efficacious throughout  $T$  and further increases in refuge will tend to increase pest pressure without increasing the efficacy of Bt corn, resulting in the left-hand side of Equation (14) becoming negative as  $ENPV$  starts to fall. Increasing refuge decreases the likelihood of resistance. If one or more of the biological constraints is binding, the right-hand side of Equation (14) will be negative. Decreases in the acceptable level of resistance or the error rate will generally require increases in refuge that decrease  $ENPV$ . Therefore, refuge recommendations that favor the first objective run contrary to the second objective, resulting in an important trade-off that must be considered by policy makers when making refuge recommendations.

### Model Implementation

The complex dynamics associated with managing both the ECB and resistance are further complicated by the consideration of multiple toxins with two distinct genetic mechanisms for resistance. Analytic treatments provide only superficial insight into the trade-off between the risk of resistance and the value of agricultural production. Much more can be learned about the relative magnitude of these trade-offs by imposing additional structure on the model and using computer simulations.

### The Evolution of Resistance

A single Bt corn event was offered for production in 1996 representing approximately 1 percent of total U.S. corn acreage. Additionally, small-scale field tests were conducted prior to 1996. In 1997,

four different Bt events were available for production representing approximately 5 percent of U.S. corn acreage.<sup>5</sup> Given the limited plantings of Bt corn, we are not aware of a confirmed case of field-level resistance prior to the 1998 growing season, which is expected assuming resistance is currently rare. In the absence of more compelling empirical evidence, we use the Hardy-Weinberg principle to characterize resistance following the work of Gould (1998), Onstad and Gould (1998a, b), and Roush and Osmond (1996).<sup>6</sup>

Let  $R_{tg}^{\vartheta}$  be the frequency of resistant alleles for the  $\vartheta$ th gene such that  $R_{tg}^a = \Gamma_{tg}^{R^a|R^b} + \Gamma_{tg}^{R^a|S^b}$  and  $R_{tg}^b = \Gamma_{tg}^{R^a|R^b} + \Gamma_{tg}^{S^a|R^b}$ . Assuming resistance genes are independent,  $\Gamma_{tg}^{R^a|R^b} = R_{tg}^a R_{tg}^b$ , implying  $\mathfrak{A}_{tg} = [R_{tg}^a R_{tg}^b, R_{tg}^a(1 - R_{tg}^b), (1 - R_{tg}^a)R_{tg}^b, (1 - R_{tg}^a)(1 - R_{tg}^b)]$ .<sup>7</sup> The Hardy-Weinberg principle implies that in the absence of selection pressure the matrix of proportions of allelic types is defined by  $\Omega_{tg} = \mathfrak{A}_{tg}' \mathfrak{A}_{tg}$ .

The Hardy-Weinberg principle assumes no selection pressure, which is not the case when Bt corn is planted. Selection pressure will depend on survival rates. Define  $\Delta_{RRg}^{\vartheta i}$ ,  $\Delta_{SSg}^{\vartheta i}$ , and  $\Delta_{RSg}^{\vartheta i} \in [0.0, 1.0]$  as the proportion of resistant and susceptible homozygotes and heterozygotes for gene  $\vartheta$  and generation  $g$  that survive on the  $i$ th crop. With these general survival rates, we can capture differences in survival rates between refuge and Bt corn that may be related to fitness, but again rely on an assumption of independence between toxins.<sup>8</sup> Given these survival rates, the matrix of allelic survival rates corresponding to  $\Omega_{tg}$  for the  $i$ th crop is

$$(15) \quad P_g^i = \begin{bmatrix} \rho_{RRg}^{ai} \rho_{RRg}^{bi} & \rho_{RRg}^{ai} \rho_{RSg}^{bi} & \rho_{RSg}^{ai} \rho_{RRg}^{bi} & \rho_{RSg}^{ai} \rho_{RSg}^{bi} \\ \rho_{RRg}^{ai} \rho_{RSg}^{bi} & \rho_{RRg}^{ai} \rho_{SSg}^{bi} & \rho_{RSg}^{ai} \rho_{RSg}^{bi} & \rho_{RSg}^{ai} \rho_{SSg}^{bi} \\ \rho_{RSg}^{ai} \rho_{RRg}^{bi} & \rho_{RSg}^{ai} \rho_{RSg}^{bi} & \rho_{SSg}^{ai} \rho_{RRg}^{bi} & \rho_{SSg}^{ai} \rho_{RSg}^{bi} \\ \rho_{RSg}^{ai} \rho_{RSg}^{bi} & \rho_{RSg}^{ai} \rho_{SSg}^{bi} & \rho_{SSg}^{ai} \rho_{RSg}^{bi} & \rho_{SSg}^{ai} \rho_{SSg}^{bi} \end{bmatrix}.$$

Using these survival rates to adjust for selection, the normalized allelic proportions on the  $i$ th crop are

$$\Omega_{tg}^i = \frac{\Omega_{tgxy} P_{gxy}^i}{\rho_{tg}^i} \text{ for all } x \text{ and } y \in \gamma \text{ where } \rho_{tg}^i = \sum_{x \in \gamma} \sum_{y \in \gamma} \Omega_{tgxy} P_{gxy}^i \text{ is the aggregate survival rate of}$$

all ECB on the  $i$ th crop.

The Hardy-Weinberg proportions also depend crucially on the assumption of random mating. Recent field surveys suggest, however, that mating may not be random.<sup>9</sup> The Hardy-Wienberg principle can be modified to address nonrandom mating. Let  $(1 - f)$  be the proportion of ECB that mate randomly

for  $f \in [0.0, 1.0]$ . With differences in selection pressure between refuge and Bt corn, the genetic variation of ECB that do not mate randomly will also differ, such that the gamete frequencies for the  $i$ th crop after selection are

$$(16) \quad \Gamma_{t \ g \ R^a | R^b}^i = \Omega_{t \ g \ R^a | R^b \ R^a | R^b}^i + \Omega_{t \ g \ R^a | R^b \ R^a | S^b}^i + \Omega_{t \ g \ R^a | R^b \ S^a | R^b}^i \\ + (1 - \kappa) \Omega_{t \ g \ R^a | R^b \ S^a | S^b}^i + \kappa \Omega_{t \ g \ R^a | S^b \ S^a | R^b}^i,$$

$$(17) \quad \Gamma_{t \ g \ R^a | S^b}^i = \Omega_{t \ g \ R^a | R^b \ R^a | S^b}^i + \Omega_{t \ g \ R^a | S^b \ R^a | S^b}^i + \Omega_{t \ g \ S^a | S^b \ R^a | S^b}^i \\ + (1 - \kappa) \Omega_{t \ g \ R^a | S^b \ S^a | R^b}^i + \kappa \Omega_{t \ g \ R^a | R^b \ S^a | S^b}^i,$$

$$(18) \quad \Gamma_{t \ g \ S^a | R^b}^i = \Omega_{t \ g \ S^a | R^b \ S^a | R^b}^i + \Omega_{t \ g \ R^a | R^b \ S^a | R^b}^i + \Omega_{t \ g \ S^a | S^b \ S^a | R^b}^i \\ + (1 - \kappa) \Omega_{t \ g \ R^a | S^b \ S^a | R^b}^i + \kappa \Omega_{t \ g \ R^a | R^b \ S^a | S^b}^i, \text{ and}$$

$$(19) \quad \Gamma_{t \ g \ S^a | S^b}^i = \Omega_{t \ g \ S^a | S^b \ S^a | S^b}^i + \Omega_{t \ g \ S^a | S^b \ R^a | S^b}^i + \Omega_{t \ g \ S^a | S^b \ S^a | R^b}^i \\ + (1 - \kappa) \Omega_{t \ g \ R^a | R^b \ S^a | S^b}^i + \kappa \Omega_{t \ g \ R^a | S^b \ S^a | R^b}^i.$$

where  $\kappa \in [0.0, 0.5]$  is the recombination factor that adjusts for linkage between the genes (see Hartl 1988). For  $\kappa = 0$ , the genes are completely linked. For  $\kappa = 0.5$ , the genes are independent, as we assume.

The genetic variation in subsequent ECB populations depends on the effective proportion of refuge, survival rates, the proportion of nonrandom mating, and differences in genetic variation between randomly and nonrandomly mated ECB. Assuming the ECB distributes uniformly across the region after mating, the proportion of allelic types in the subsequent generation is

$$(20) \quad \Omega_{t1} = f n_{t-12}^{Non} \Gamma_{t-12}^{Non} \Gamma_{t-12}^{Non} \\ + f (1 - n_{t-12}^{Non}) \Gamma_{t-12}^{Bt} \Gamma_{t-12}^{Bt} \\ + (1 - f) \left[ \left( n_{t-12}^{Non} \Gamma_{t-12}^{Non} + (1 - n_{t-12}^{Non}) \Gamma_{t-12}^{Bt} \right) \left( n_{t-12}^{Non} \Gamma_{t-12}^{Non} + (1 - n_{t-12}^{Non}) \Gamma_{t-12}^{Bt} \right) \right], \text{ and}$$

$$(21) \quad \Omega_{t2} = f n_{t1}^{Non} \Gamma_{t1}^{Non} \Gamma_{t1}^{Non} \\ + f (1 - n_{t1}^{Non}) \Gamma_{t1}^{Bt} \Gamma_{t1}^{Bt} \\ + (1 - f) \left[ \left( n_{t1}^{Non} \Gamma_{t1}^{Non} + (1 - n_{t1}^{Non}) \Gamma_{t1}^{Bt} \right) \left( n_{t1}^{Non} \Gamma_{t1}^{Non} + (1 - n_{t1}^{Non}) \Gamma_{t1}^{Bt} \right) \right],$$

where  $n_{t1}^{Non} = \frac{\phi_t^e \rho_{t1}^{Non}}{\phi_t^e \rho_{t1}^{Non} + (1 - \phi_t^e) \rho_{t1}^{Bt}}$  and  $n_{t-12}^{Non} = \frac{\phi_{t-1}^e \rho_{t-12}^{Non}}{\phi_{t-1}^e \rho_{t-12}^{Non} + (1 - \phi_{t-1}^e) \rho_{t-12}^{Bt}}$  is the proportion of

surviving pest emerging from refuge in the first and second generations. Equations (20) and (21) are the



weighted average of allelic proportions based on the effective size of refuge, relative survival rates on refuge and Bt corn, and the proportion of randomly mating ECB.

Currently, research is being conducted to estimate the value of  $f$ . For our benchmark model we focus on  $f = 0$ , but we also explore the consequences of nonrandom mating by considering  $f = 0.20$ .

### Pest Survival Rates

The level of toxin expressed by Bt corn has been found to differ by event. Some events, for instance, do not express Bt throughout the season reducing their effectiveness on second generation ECB. Most events, however, provide full-season control that does not differ significantly between first and second generation ECB. To limit the scope of our analysis, we focus on events that provide full-season control and no longer differentiate between the survival rates of first and second generation ECB:  $\Delta_{RR}^{\vartheta i} = \Delta_{RRg}^{\vartheta i} = \Delta_{RRg}^{\vartheta i}$ ;  $\Delta_{SS}^{\vartheta i} = \Delta_{SSg}^{\vartheta i} = \Delta_{SSg}^{\vartheta i}$ ; and  $\Delta_{RS}^{\vartheta i} = \Delta_{RSg}^{\vartheta i} = \Delta_{RSg}^{\vartheta i}$ .

To further maintain a more manageable focus, we impose some additional simplifying assumptions on the survival rates that have been used by others. First, assume that resistance confers no fitness costs, which allows us to normalize our survival rates to one for all ECB on refuge:  $\Delta_{RR}^{\vartheta Non} = \Delta_{RS}^{\vartheta Non} = \Delta_{SS}^{\vartheta Non} = 1.0$ .<sup>10</sup> Second, assume that the toxin selecting for the  $\vartheta$ th gene kills all susceptible homozygotes:  $\Delta_{SS}^{\vartheta Bt} = 0.0$ . Third, assume that resistance is complete, such that all resistant homozygotes for  $\vartheta$  survive on Bt corn that selects for  $\vartheta$ :  $\Delta_{RR}^{\vartheta Bt} = 1.0$ . What remains to be defined is the survival rate of heterozygotes. If the high-dose strategy is effective and resistance is a recessive trait, all ECB that are heterozygous for  $\vartheta$  will perish on Bt corn that selects for  $\vartheta$ . However, if resistance is only partially recessive, as some entomologists suspect, some ECB that are heterozygous for  $\vartheta$  will survive on Bt corn that selects for  $\vartheta$ . Therefore, we do not restrict the survival rates of heterozygotes on Bt corn a priori:  $\Delta_{RS}^{\vartheta Bt} \in [0.0, 1.0]$ .

### Effective Refuge

Not all refuge recommendations are mandatory and even mandatory recommendations are hard to enforce. So compliance with refuge recommendations has become an important issue. Furthermore, some producers may choose not to plant Bt corn depending on the premium charged by industry and the perceived threat of ECB damage.

Although industry has conducted extensive research to determine adoption rates for Bt corn, this information is proprietary and generally not made available publicly for competitive reasons. Therefore, we assume that the entire region is planted to a single Bt corn event with the exception of refuge. This

worst case scenario will ultimately result in an upward bias in the refuge recommendation, but there is no reason to suspect a qualitative bias with regard to sources of controversy that we explore.

Industry has also conducted surveys to assess producer compliance with refuge recommendations and has found that producers report they were less willing to accept higher refuge recommendations. These results make sense because as the refuge recommendation increases so does a producer's cost of compliance. However, compliance decisions are not made exclusively based on economic costs. The perceived legitimacy of the recommendation and social norms can influence whether or not a producer complies. To better understand the consequences of grower compliance, we incorporate a compliance function that adjusts the refuge recommendation to the effective refuge size:

$$(22) \quad \phi_t^e = \phi e^{-\eta \phi}.$$

Equation (22) allows producer noncompliance to reduce the effective size of refuge. If  $\eta = 0$ , producers fully comply with the recommendation. If  $\eta > 0$ , the effective size of refuge will decrease at a rate of  $\eta$  as the refuge recommendation increases.

We use the results of a telephone survey conducted by Harvest Research Company to parameterize  $\eta > 0$  so we can compare scenarios of partial compliance with a benchmark model of full compliance:  $\eta > 0$  and  $\eta = 0$ . The survey asked 504 producers who had planted Bt corn across the central United States, "If the 5 percent minimum unsprayed refuge were increased, would this new level be acceptable?" The alternative refuge recommendations considered were 10, 15, 20, 25, and 30 percent, of which 86, 62, 46, 31, and 21 percent out of 370 producers agreed. A producer's failure to accept a particular increase in the refuge recommendation will not be perfectly correlated with his decision to comply. Social norms and the perceived legitimacy of the recommendation may convince some producers to comply even if they find the recommendation unacceptable. Therefore, these numbers may overstate the level of noncompliance. Still, the survey provides tangible evidence that can be used to calculate a rate of compliance for comparison purposes. Taking the log of the proportion of acceptance, we use a linear regression to estimate  $\eta = 4.42$  with a standard error of 0.40 and an  $R^2$  of 0.90.

### **Costs and Revenues**

We use National Agricultural Statistical Service (NASS) and Economic Research Service (ERS) data to calculate reasonable economic parameter values for the real price of corn, the pest-free yield, and

production costs. The real price of corn, \$2.35, was calculated using NASS monthly average corn prices in the United States from 1991 to 1996 deflated to 1992.<sup>11</sup> The average Iowa yield reported by NASS from 1991 to 1996 was about 123 bushels per acre. Assuming an average annual ECB yield loss of 6.4 percent (Calvin 1996) implies an average annual pest-free yield of about 130 bushels per acre. Excluding returns to management, the average production costs for refuge corn, \$185, were calculated with 1995 ERS corn budgets deflated to 1992 using NASS price indices. Most of the increased cost of producing Bt corn is fixed research and development costs. Although industry currently charges about \$10 an acre more for Bt seed corn, this premium does not reflect the increased marginal cost of producing Bt corn. The major difference in the production of Bt events and non-Bt isolines is that Bt events are subject to more rigorous quality control measures (personal communications with Jonathan B. Sagers, Novartis Seeds; Dr. Paula M. Davis, Monsanto Company; and Dr. Rod Townsend, Pioneer Hi-Bred International, Inc.). Therefore, while the marginal production costs of Bt events may be higher than refuge, exactly how much higher is not clear. To focus on the resistance management benefits of Bt corn, we assume that the difference in production costs is negligible. A real interest rate of 4 percent is also assumed.

Damage estimates for the ECB vary depending on a variety of environmental and management factors. For instance, damages will be higher when corn is stressed and in early or late-planted corn. Depending on a plant's stage of development, estimates indicate a marginal yield loss ranging from 2 to 6 percent pests/plant (Mason et al. 1996). Since our interest is in evaluating the average seasonal damage of the ECB over a production region, we assume

$$(23) \quad D_t^i = d_1 N_{t1}^i + d_2 N_{t2}^i$$

where  $d_g$  is the constant marginal proportion of yield loss pests/plants. Based on Mason et al. (1996) we set  $d_g = 0.04$  for  $g = \{1, 2\}$  as a baseline estimate.

Hurley et al. (1997) show that the refuge recommendation is sensitive to the length of the planning horizon,  $T$ . The ILSI-HESI report explicitly defines the length of the planning horizon for preserving pest susceptibility to be 30 generations or 15 years for bivoltine ECB. This 15-year planning horizon is not without controversy for events that express a single toxin because new multiple toxin events could be available within five to ten years. If these multiple toxin events displace single toxin events, a shorter planning horizon may be reasonable. Therefore, while our benchmark model focuses on a 15-year planning horizon as specified by the ILSI-HESI report, we compare the results for a 15-year planning horizon to a five-year planning horizon.

### ECB Population Uncertainty

ECB populations are quite variable due to a number of environmental factors. Attempts to develop predictive models for producers to make better management decisions based on past ECB populations have generally resulted in frustration and in the conclusion that populations are random for the most part. In the past, however, the ECB has not been subject to the intensity and persistence of the type of selection pressure Bt corn can impose. The degree to which Bt corn suppresses ECB populations within a region will affect the resistance management benefits of refuge, but it is not immediately clear how the degree of ECB suppression should influence refuge recommendations.

We explore two different types of ECB population models to better understand the effect of pest suppression on the agricultural benefits of Bt corn. The first assumes the ECB population is random but depends on the previous generation's population such that planting Bt corn can suppress the ECB population. The second assumes the ECB population is completely random and will not be suppressed by Bt corn.

The apparent randomness of ECB populations has generally discouraged the collection of longitudinal ECB larvae data. Most recent collection efforts focus on quantifying ECB tunneling or moth flights. Unfortunately, end-of-season tunneling data does not allow for distinctions between generations, while moth flight data is difficult to calibrate to field-level populations. An older collection effort conducted between 1960 and 1969 provides more suitable information for our analysis (see Calvin 1996).

The 1960s ECB population data includes the number of first and second-generation ECB larvae per plant at six sites across the Midwest. At four of the sites data was collected for the full ten-year period. At the remaining two sites, data was collected for four and five years. Pooling the data, the average number of ECB per plant was 0.14 for the first generation and 0.95 for the second generation, resulting in an average annual population of just over one ECB per plant.

Assuming the ECB population in a generation is log-normally distributed with the mean and variance of the underlying normal distribution of  $\mu_{N_g}$  and  $\Phi_{N_g}^2$ , we pool the data and use the maximum likelihood procedure to estimate the underlying parameters of the distribution. For the first model, we assume  $\mu_{N_1} = \beta_0^1 + \beta_1^1 N_{t-1,2}^S + \beta_2^1 N_{t-1,2}^{S^2}$ ,  $\mu_{N_2} = \beta_0^2 + \beta_1^2 N_{t,1}^S + \beta_2^2 N_{t,1}^{S^2}$  and  $\Phi_{N_g}^2 = \forall_0^g$ , whereas for the second, we assume  $\mu_{N_g} = \beta_0^g$  and  $\Phi_{N_g}^2 = \forall_0^g$ . The quadratic form for the mean of our first population model places an upper bound on the population mean if the coefficient estimates are positive for the linear terms and negative for quadratic terms.

Table 2 reports the maximum likelihood coefficient estimates, the maximized value of the likelihood function, and the log-likelihood ratio test comparing the two models. The log-likelihood ratio test is

significant at a one 1 percent level of confidence suggesting that current populations are dependent on previous populations and that high adoption rates for Bt corn could suppress the ECB population. Therefore, we use model 1 as our benchmark. As expected, coefficient estimates are positive for the linear terms and negative for the quadratic terms. Table 3 (B) shows the long-run implications of our population models when there is no selection pressure from Bt corn. For model 1, the average annual population is 1.10 pest per plant with a standard deviation of 0.50. For model 2, the average annual population is 1.35 pest per plant with a standard deviation of 0.63.

Table 2: Parameter estimates for ECB population models

	Coefficient	Model 1	Model 2
<i>First Generation</i>			
	Constant	-3.52 <sup>a</sup> (0.310)	-2.50 <sup>a</sup> (0.188)
	Previous Surviving Population	1.81 <sup>b</sup> (0.720)	
	Previous Surviving Population <sup>2</sup>	-0.39 (0.267)	
	Standard Deviation	0.96 <sup>a</sup> (0.136)	1.17 <sup>a</sup> (0.199)
<i>Second Generation</i>			
	Constant	-1.59 <sup>a</sup> (0.300)	-0.66 <sup>a</sup> (0.211)
	Previous Surviving Population	9.47 <sup>b</sup> (4.481)	
	Previous Surviving Population <sup>2</sup>	-11.31 (10.897)	
	<b>I.</b> Standard Deviation	1.11 <sup>a</sup> (0.128)	1.28 <sup>a</sup> (0.134)
	Maximized Log-Likelihood	5.99	-10.01
	$\Pi^2(4)$	32.00 <sup>a</sup>	
	Observations	92	92

Notes: Standard errors are in parentheses, <sup>a</sup>denotes a 1 percent level of significance, <sup>b</sup>denotes a 5 percent level of significance, and <sup>c</sup>denotes a 10 percent level of significance.

Table 3: Summary of (A) parameter values and (B) distributions

A					
Parameter Name			Benchmark Value/ Other Values		
<i>Biological Parameters</i>					
Generations of Pests Per Cropping Season			2		
Resistant Homozygote Survival Rate for Both Genes			1.0		
Susceptible Homozygote Survival Rate on Refuge for Both Genes			1.0		
Susceptible Homozygote Survival Rate on Bt Corn for Both Genes			0.0		
Heterozygotes Survival Rate on Refuge for Both Genes			1.0		
Proportion of Nonrandom Mating			0.0/0.20		
Initial Pest Population (Pests Per Plant)			0.23		
Number of Independent Toxins Expressed by Bt Corn			1/2		
Resistance Threshold for Gene <i>a</i> ( $\theta^a$ )			0.50		
Resistance Threshold for Gene <i>a</i> ( $\theta^b$ )			0.50		
Resistance Threshold for Gene <i>a</i> and <i>b</i> ( $\theta^{ab}$ )			0.50		
<i>Economic Parameters</i>					
Planning Horizon (Years)			15/5		
Noncompliance Rate			0.0/4.42		
Interest Rate			0.04		
Price of Corn Per Bushel			\$2.35		
Pest-Free Yield for Bt Corn and Refuge (Bushels Per Acre)			130		
Production Cost for Bt Corn and Refuge (Per Acre)			\$185.00		
Constant Marginal Yield Loss for Both Generations (Pests Per Plant)			0.04		
B					
Parameter	Mean	Standard Deviation	95 <sup>th</sup> Percentile	Correlation	
<i>Gene a</i>					
Initial Frequency of Resistant Alleles	3.2×10 <sup>-4</sup>	4.4×10 <sup>-4</sup>	1.3×10 <sup>-3</sup>	-0.49	
Heterozygote Survival on Bt Corn	0.020	0.025	0.078		
<i>Gene b</i>					
Initial Frequency of Resistant Alleles	3.2×10 <sup>-4</sup>	4.4×10 <sup>-4</sup>	1.3×10 <sup>-3</sup>	-0.49	
Heterozygote Survival on Bt Corn	0.020	0.025	0.078		
<i>Pest Population with 100 Percent Refuge (Pest/Plant)</i>					
Model 1 (Benchmark)	1.10	0.50	2.01		
Model 2	1.35	0.63	2.41		

Given the allelic survival rates previously discussed, the surviving pest population is explicitly defined as

$$(24) \quad N_{t1}^S = [N_t^e \rho_{t1}^{Non} + (1 - N_t^e) \rho_{t1}^{Bt}] N_{t1}, \text{ and}$$

$$(25) \quad N_{t2}^S = [N_t^e \rho_{t2}^{Non} + (1 - N_t^e) \rho_{t2}^{Bt}] N_{t2}.$$

### Resistance and Survival Uncertainty

Prior to the 1998 growing season, we are not aware of a confirmed case of an ECB surviving on Bt corn even with a number of ambitious monitoring programs currently in place. This suggests that resistance is rare and that the heterozygote survival rate is most likely small. However, it is still not clear exactly how rare or how small.

Field-level monitoring can provide useful information on the likelihood of resistance and heterozygote survival rates. By sampling Bt corn plants and adjacent non-Bt isolines, the relative survival rate of ECB on Bt corn can be obtained. These survival rates can then be used to quantify the likelihood of current levels of resistance and the survival rate of heterozygotes on Bt corn.

Define  $M$  as the number of fields surveyed,  $z_k$  as the observed survival rate on Bt corn relative to an adjacent non-Bt isolate, and  $m_k$  as the number of observations taken from the  $k$ th field for  $k = 1, \dots, M$ . As  $m_k$  becomes large, the central limit theorem implies the survival rate will be normally distributed with mean  $\mu_z$  and variance  $\sigma_z^2$ . For a single toxin event that selects for resistance at gene  $\tau$ , the expected survival rate will be  $\mu_z = R^\tau + 2\Delta_{RS}^\tau R^\tau(1 + R^\tau)$  where  $R^\tau$  is the current proportion of resistant alleles and  $\Delta_{RS}^\tau$  is the heterozygote survival rate on Bt corn. Also, assume  $\sigma_z^2 = \sigma_z^2 m_k^{-1}$ , which implies a common sampling error that decreases with the sample size.

Our goal is to be able to identify the distribution of  $R^\tau$  and  $\Delta_{RS}^\tau$  given both prior information and new information from the field. Because we only have one piece of information to identify two parameters, we rely on Bayesian methods. Bayes rule implies

$$(26) \quad \Pr(R^\tau, \rho_{RS}^\tau, \sigma_z^2 | z_1, \dots, z_M) \propto \Pr(R^\tau, \rho_{RS}^\tau, \sigma_z^2) \Pr(z_1, \dots, z_M | R^\tau, \rho_{RS}^\tau, \sigma_z^2)$$

where  $\Pr(R^\tau, \Delta_{RS}^\tau, \sigma_z^2)$  is the probability of  $R^\tau$ ,  $\Delta_{RS}^\tau$ , and  $\sigma_z^2$  given prior information and  $\Pr(z_1, \dots, z_M | R^\tau, \Delta_{RS}^\tau, \sigma_z^2)$  is the likelihood of observing  $z_1$  through  $z_M$  given  $R^\tau$ ,  $\Delta_{RS}^\tau$ , and  $\sigma_z^2$ :

$$\begin{aligned}
(27) \quad \Pr(z_1, \dots, z_M \mid R^\tau, \rho_{RS}^\tau, \sigma_z^2) &= \prod_{k=1}^M \frac{m_k}{\sigma_z^2 \sqrt{2\pi}} e^{-\frac{m_k (z_k - \mu_z)^2}{2\sigma_z^2}} \\
&= \sigma_z^{2M} (2\pi)^{-\frac{M}{2}} \prod_{k=1}^M m_k e^{-\sum_{k=1}^M \frac{m_k (z_k - \mu_z)^2}{2\sigma_z^2}}.
\end{aligned}$$

Since we have no information on  $\sigma_z^2$  to base a prior, we can simplify Equation (26) by assuming  $\sigma_z^2$  is independent of  $R^\tau$  and  $\Delta_{RS}^\vartheta$  and has uninformed prior such that  $\Pr(\sigma_z^2) \propto 1/\sigma_z^2$  (see Lee 1997, pp. 45-46). This results in

$$(28) \quad \Pr(R^\tau, \rho_{RS}^\tau \mid z_1, \dots, z_M) \propto \Pr(R^\tau, \rho_{RS}^\tau) \left( \sum_{k=1}^M m_k (z_k - \mu_z) \right)^{-\frac{M}{2}},$$

where  $\Pr(R^\tau, \Delta_{RS}^\vartheta)$  is the joint probability of  $R^\tau$  and  $\Delta_{RS}^\vartheta$  given prior information and  $\Pr(R^\tau, \Delta_{RS}^\vartheta \mid z_1, \dots, z_M)$  is the joint probability of  $R^\tau$  and  $\Delta_{RS}^\vartheta$  combining new information with prior information. With the appropriate field data and a distribution for  $\Pr(R^\tau, \Delta_{RS}^\vartheta)$  we can use numerical methods to estimate the expected net present value of agricultural production and the probability of resistance given the refuge recommendation.

The field data we use comes from 1997 field surveys conducted by Monsanto. We initially considered 101 nonirrigated unsprayed fields across the Midwest. Of these 101 fields only seven had positive survival rates. Since we are unaware of a confirmed case of resistance in the 1997 field survey, we suspect most of the ECB found surviving in these fields were surviving on plants that failed to express Bt.<sup>12</sup> Therefore, we did not consider four of the observations that had survival rates in excess of 4 percent and we adjusted the remaining survival rates assuming that 2 percent of the plants in Bt fields failed to express Bt. In summary, the data we used consisted of 6,450 plants sampled from 97 different fields with an average survival rate of  $2.2 \times 10^{-6}$ , which is consistent with a more exhaustive survey of ECB survivorship on Bt corn conducted in Illinois (Weinzierl et al. 1997).

Andow and Alstad (1998) report on a laboratory technique called the  $F_2$  screen for deriving an upper bound on resistant allele frequencies. Recent estimates calculated using data from Iowa suggest that  $\Pr(R^\tau < 4.38 \times 10^{-3}) = 0.95$ . Less is known about the heterozygote survival rate. The ILSI-HESI report assumes that  $\Delta_{RS}^\vartheta < 0.10$ . While the  $\Pr(R^\tau, \Delta_{RS}^\vartheta \mid z_1, \dots, z_M)$  is sensitive to  $\Pr(R^\tau, \Delta_{RS}^\vartheta)$ , this sensitivity diminishes as the sample size increases. For the analysis that follows, we use



$$(29) \quad \Pr(R^\tau, \rho_{RS}^\tau | z_1, \dots, z_M) \propto \frac{1}{4.61 \times 10^{-3}} \frac{1}{0.1} \left( \sum_{k=1}^M m_k (z_k - \mu_z) \right)^{\frac{M}{2}},$$

which implies the prior distribution for the initial frequency of resistant alleles is uniformly distributed satisfying  $\Pr(R^\tau < 4.38 \times 10^{-3}) = 0.95$  and independent of the uniformly distributed prior for the heterozygote survival rate that is assumed to lie on the interval  $[0.0, 0.10]$ .

Using Equation (29) yields an average resistant allele frequency of  $3.2 \times 10^{-4}$  with a standard deviation of  $4.4 \times 10^{-4}$  and 95<sup>th</sup> percentile of  $1.3 \times 10^{-3}$  (Table 3 (B)). The average heterozygote survival rate is 0.02 with a standard deviation of 0.025 and a 95<sup>th</sup> percentile of 0.078. The correlation between the initial resistance frequency and the heterozygote survival rate is  $-0.49$ . This strong negative correlation indicates that a higher initial resistance frequency is more consistent with low observed survival rates when the heterozygote survival rate is lower, or conversely, that a higher heterozygote survival rate is more consistent with low observed survival rates when the initial resistance frequency is lower. We use Equation (29) to characterize resistant allele frequencies and heterozygote survival rates for both genes independently.

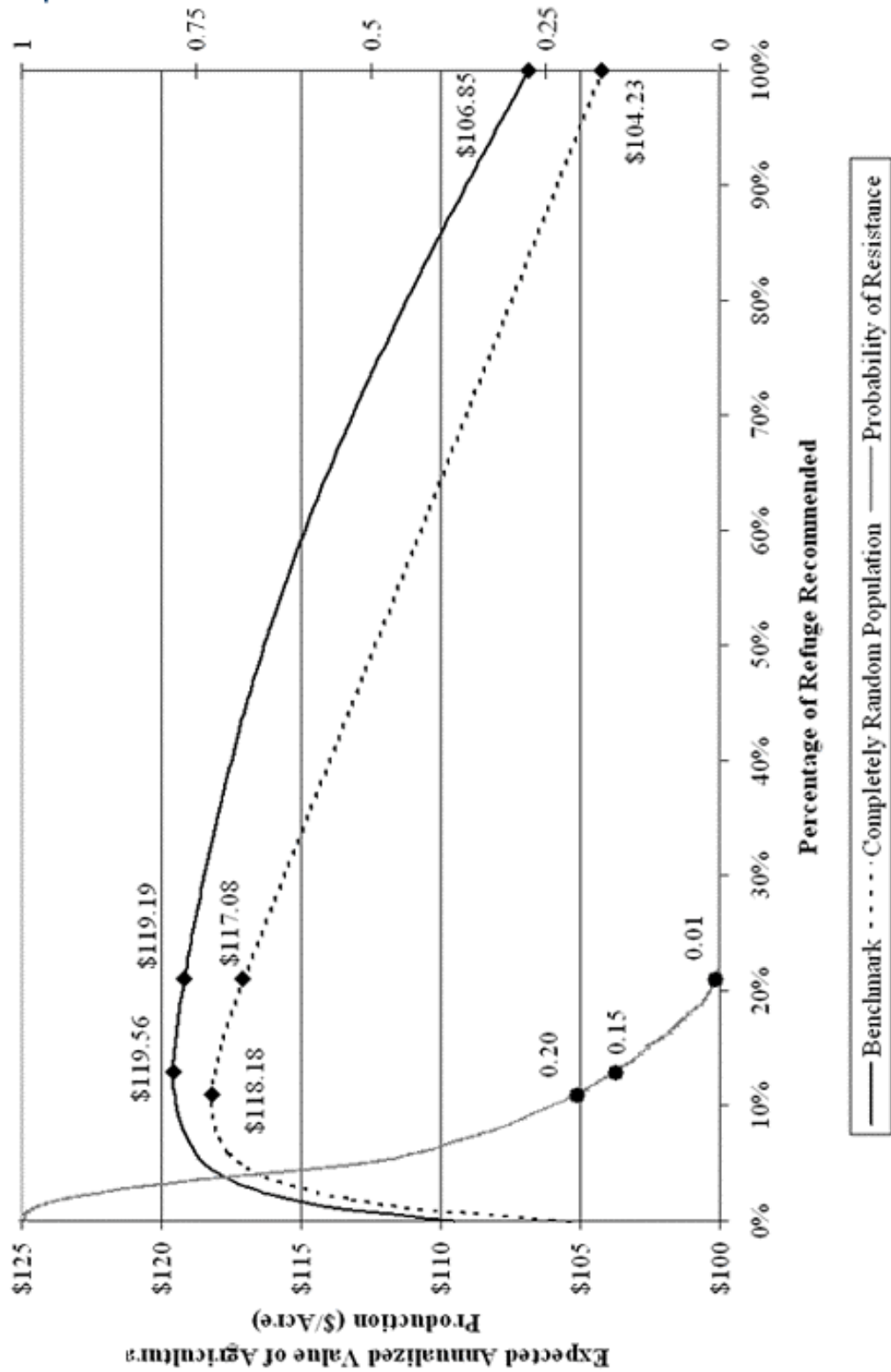
## Results

Reviewing the debate over refuge recommendations, we focus on four issues of debate: (a) the value of reducing the risk of resistance, (b) the potential introduction of new multiple toxin plants, (c) producer compliance, and (d) the degree of nonrandom mating. We now explore these points of debate by comparing a benchmark model with alternative scenarios that incorporate the various issues of contention. Table 2 (A) and (B) summarizes the information used to parameterize and run the benchmark model and alternative parameter values that are explored.

### Pest Susceptibility versus Agricultural Production

The two important objectives that have been identified for refuge recommendations are the maintenance of pest susceptibility and the agricultural benefits of Bt corn. Figure 1 shows the relationship between the refuge recommendation, the expected annualized net present value of agricultural production per acre, and the probability that the frequency of resistant alleles exceeds 0.50 for our benchmark model.<sup>13</sup> Figure 1 also shows the expected value of agricultural production when the benchmark population model is replaced with the completely random model where suppression does not occur.

**Figure 1. Agricultural Production and Resistance Comparison for Alternative Population Models.**



Increasing refuge initially increases the value of agricultural production because although more refuge tends to increase ECB pressure, it also slows the development of resistance allowing the ECB to be effectively controlled longer. Once ECB control is established in the long run, however, further increases in refuge reduce the value of agricultural production because the increase in ECB pressure due to a larger refuge no longer provides significant benefits by improving the efficacy of Bt corn. Increases in refuge decrease the probability of resistance. But once refuge exceeds approximately 20 percent, further increases in refuge decrease the probability of resistance negligibly.

The appropriate refuge recommendation depends crucially on the importance that is placed on maintaining pest susceptibility relative to maintaining the production value of Bt corn. Industry and producers place more emphasis on the value of production and tend to favor lower refuge recommendations because they currently bear the increased financial cost of preserving pest susceptibility. Policy makers must determine to what degree decreasing the risk of resistance is worth reducing the value of agricultural production.

The value of agricultural production is maximized with a refuge recommendation of 13 percent when ECB suppression occurs and approximately 11 percent when the ECB population is completely random. Comparing the value of agricultural production at these recommendations with the value of agricultural production when no Bt corn is planted yields the expected annual values of Bt corn over the 15-year planning horizon, \$12.71 and \$13.95 per acre. Note that the value of Bt corn is almost 10 percent higher if it does not suppress the ECB because average populations tend to be higher.

The probability of resistance is 0.15 and 0.20 at the refuge recommendations that maximize the value of agricultural production for the different population models. If this is deemed unacceptable, the refuge recommendation can be increased to reduce the probability of resistance. Increasing the refuge recommendation to about 21 percent reduces the probability of resistance to less than 1 percent; however, it also reduces the value of agricultural production. For the benchmark model, increasing refuge from 13 to 21 percent decreases the value of production from about \$119.56 to \$119.19, which is approximately 3 percent of the value of the technology. When ECB populations are not suppressed, increasing refuge from 11 to 21 percent decreases the value of production from \$118.18 to \$117.08, which is approximately 8 percent of the value of the technology.

Refuge recommendations below 13 percent for the benchmark model make little sense because the value of production decreases, while the probability of resistance increases. Refuge recommendations above 21 percent also make less sense because little is gained in terms of reducing the probability of resistance, while the value of agricultural production steadily declines. Between 13 and 21 percent, the

appropriate recommendation depends on how much risk of resistance policy makers will accept in exchange for greater agricultural productivity.

### **Multiple Independent Toxins**

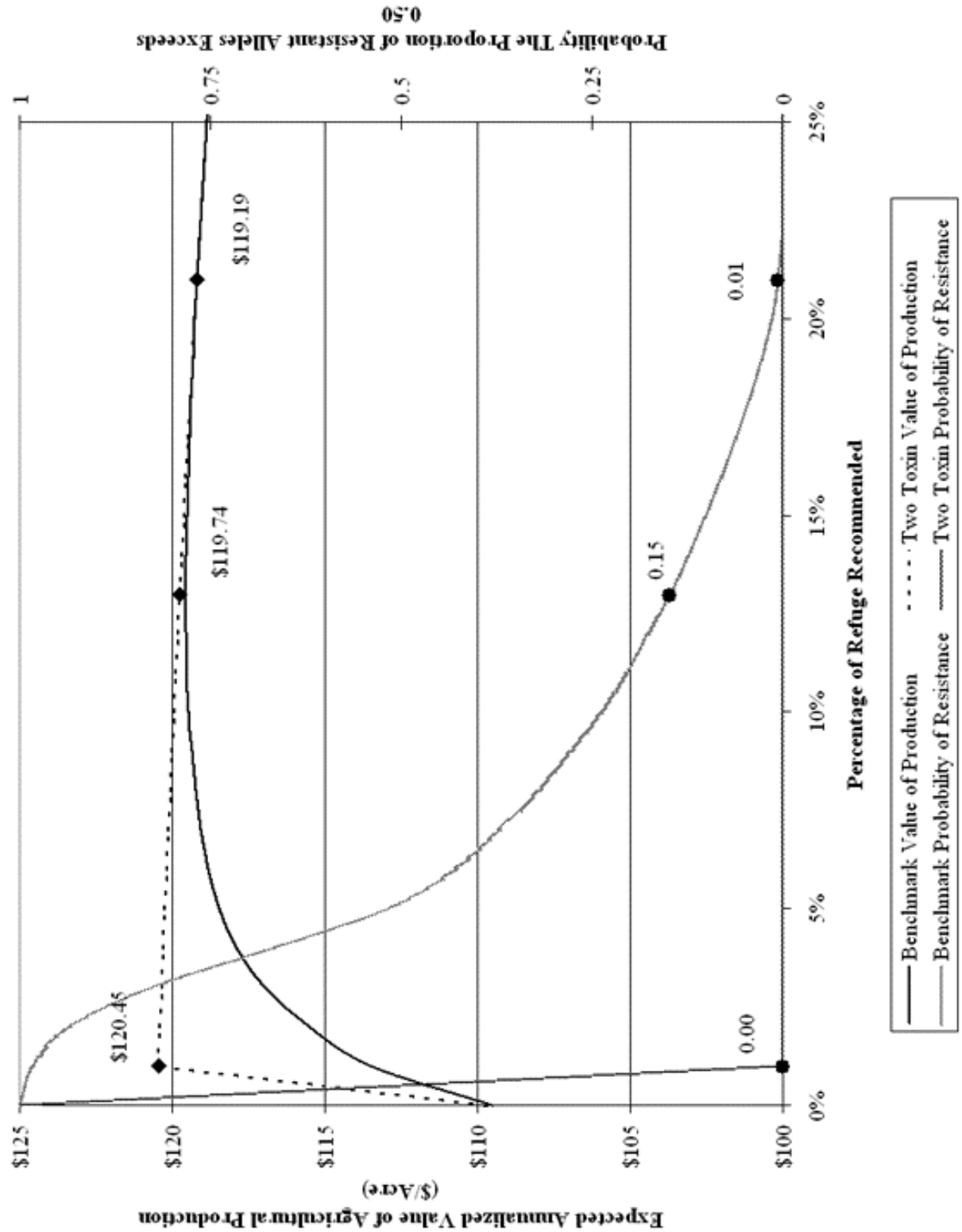
Varieties of Bt corn that express two toxins were field tested in 1998. If the toxins are independent and novel, Figure 2 shows these new varieties can provide significant resistance management benefits by reducing the amount of refuge necessary to maintain pest susceptibility and the value of agricultural production. For the two-toxin event in Figure 2, the value of agricultural production is maximized with about 1 percent refuge. One percent refuge also leads to less than 1 percent chance of resistance developing to either or both toxins, which reduces controversy over the appropriate level of risk. The maximized value of agricultural production for the two-toxin event is \$120.45 per acre, resulting in a value to the technology of \$13.60 an acre.

Industry has the best information on what new events are being developed and when they will become available. This has led members of industry to favor a lower recommendation because they expect that current events will be replaced within the next 10 years, which dictates a shorter planning horizon. Entomologists and others in academia have supported a longer planning horizon and more refuge because of uncertainty regarding when new events will be available and whether or not these events will actually replace current events.

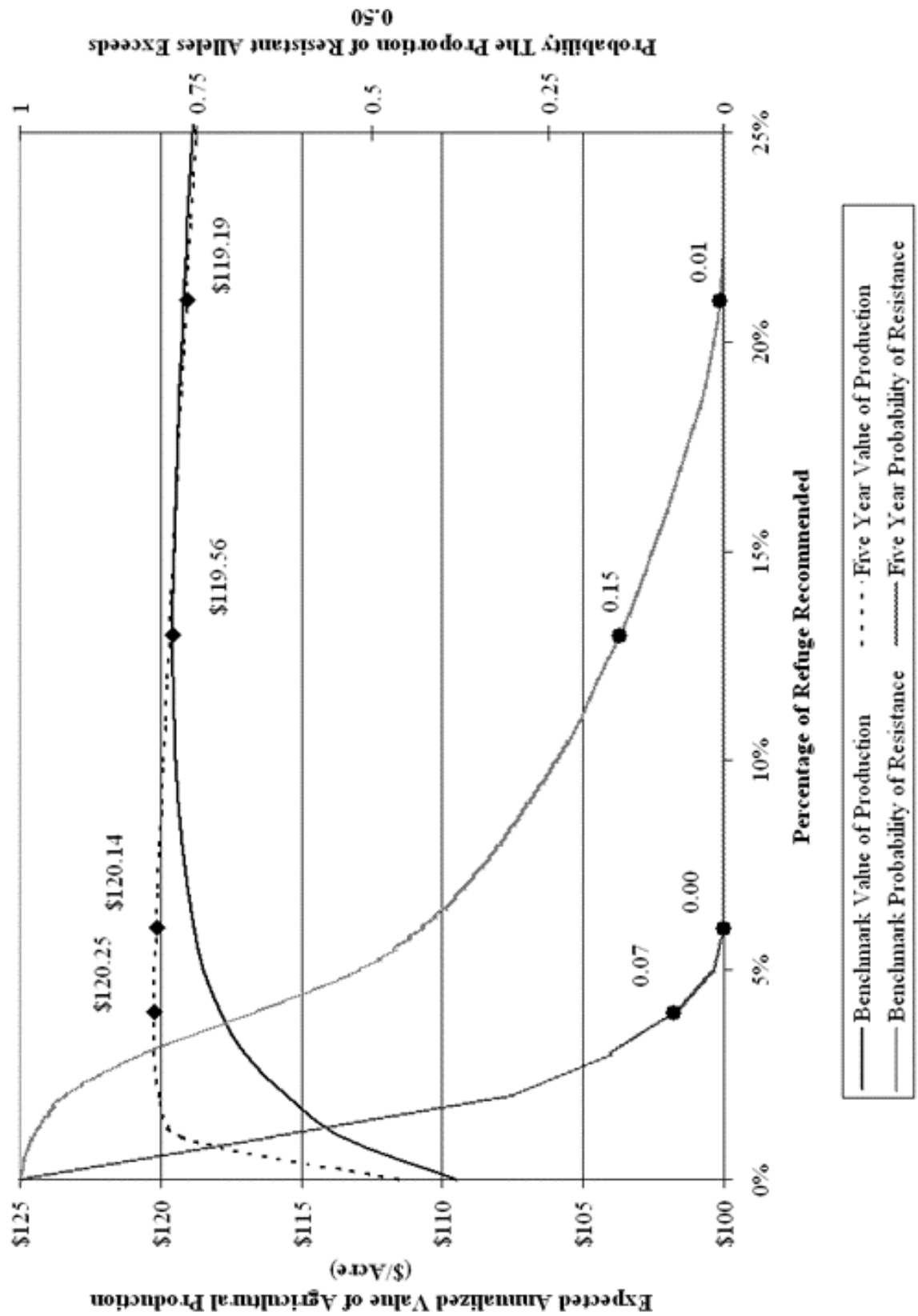
When multiple toxin plants do become available, both toxins may not be novel and single-toxin events may continue to be used by producers. Therefore, it is not immediately clear how to incorporate the potential of these new events into current recommendations. But if these new events completely replace single-toxin events before 15 years, then a shorter planning horizon may be appropriate.

Figure 3 compares the benchmark model with the 15-year planning horizon to a five-year planning horizon. If new events replace current events within five years, less refuge is needed to preserve susceptibility. For a five-year planning horizon, the value of production is maximized with 4 percent refuge, resulting in a 7 percent chance of resistance. Increasing refuge to 6 percent reduces the value of production by \$0.15 or less than 1 percent of the value of the technology and results in less than 1 percent chance of resistance. Therefore, those arguing for a shorter planning horizon will support lower refuge recommendations.

Figure 2. Agricultural Production and Resistance Comparison for Single and Multiple Toxins.



**Figure 3. Agricultural Production and Resistance Comparison for Alternative Planning Horizons.**



### **Producer Compliance**

Producer compliance with refuge recommendations will depend on the cost of compliance, the perceived legitimacy of the recommendation, and social norms. By encouraging cooperation among industry, producers, and scientists, the EPA has attempted to improve the legitimacy of the recommendations. If producers are skeptical of refuge recommendations, however, compliance may be based primarily on financial costs and decrease with higher refuge recommendation because of increased costs.

Producer noncompliance has two important implications for the design of refuge recommendations. First, a higher recommendation may be necessary to boost the effective proportion of refuge that is actually planted. Second, increases in the refuge recommendation to reduce the risk of resistance can become counterproductive as an increasing number of producers choose to ignore the recommendation. Therefore, noncompliance may dictate either a higher or lower refuge recommendation.

Figure 4 compares the benchmark model of full compliance with a model where compliance diminishes as the refuge recommendation increases. For the noncompliance model, the value of production is maximized with a 23 percent refuge recommendation that effectively results in around 8 percent refuge. Interestingly, the 23 percent recommendation also minimizes the risk of resistance, which is just above 30 percent. Increasing the refuge recommendation above 23 percent will decrease the value of production and increase the probability of resistance because greater noncompliance will reduce the amount of refuge that is actually planted.

### **Nonrandom Mating**

Originally, the high-dose refuge strategy assumed that ECB on refuge would randomly mate with ECB on Bt corn. This random mating assumption is important if refuge is to work as expected. If ECB on refuge do not mate randomly with ECB on Bt corn as recent evidence suggests, more refuge is needed to control resistance. Disagreement over the degree of random mating has thus led to differences in refuge recommendations.

For example, Figure 5 compares the benchmark model having random mating with the benchmark having only 80 percent of ECB on refuge and Bt corn mating randomly. With 20 percent nonrandom mating, the refuge recommendation that maximizes the value of production is 18 percent, five percentage points higher than with nonrandom mating. The refuge recommendation that reduces the probability of resistance below 1 percent is 25 percent for nonrandom mating as compared with 21 percent with random mating. Therefore, nonrandom mating shifts the range of sensible refuge recommendations upward while also reducing the value of Bt corn by slightly less than 3 percent.

Figure 4. Agricultural Production and Resistance Comparison for Partial and Full Compliance Models.

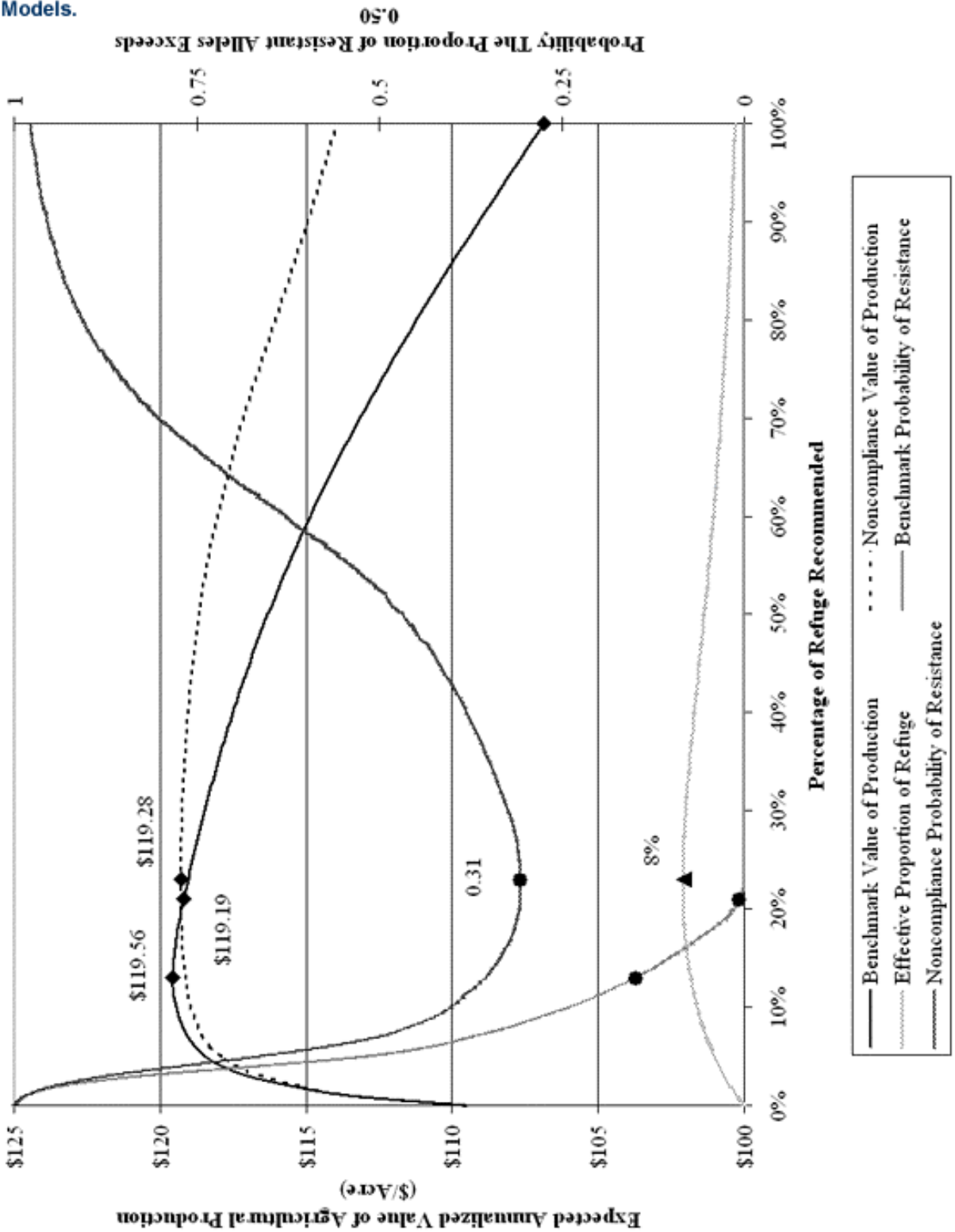
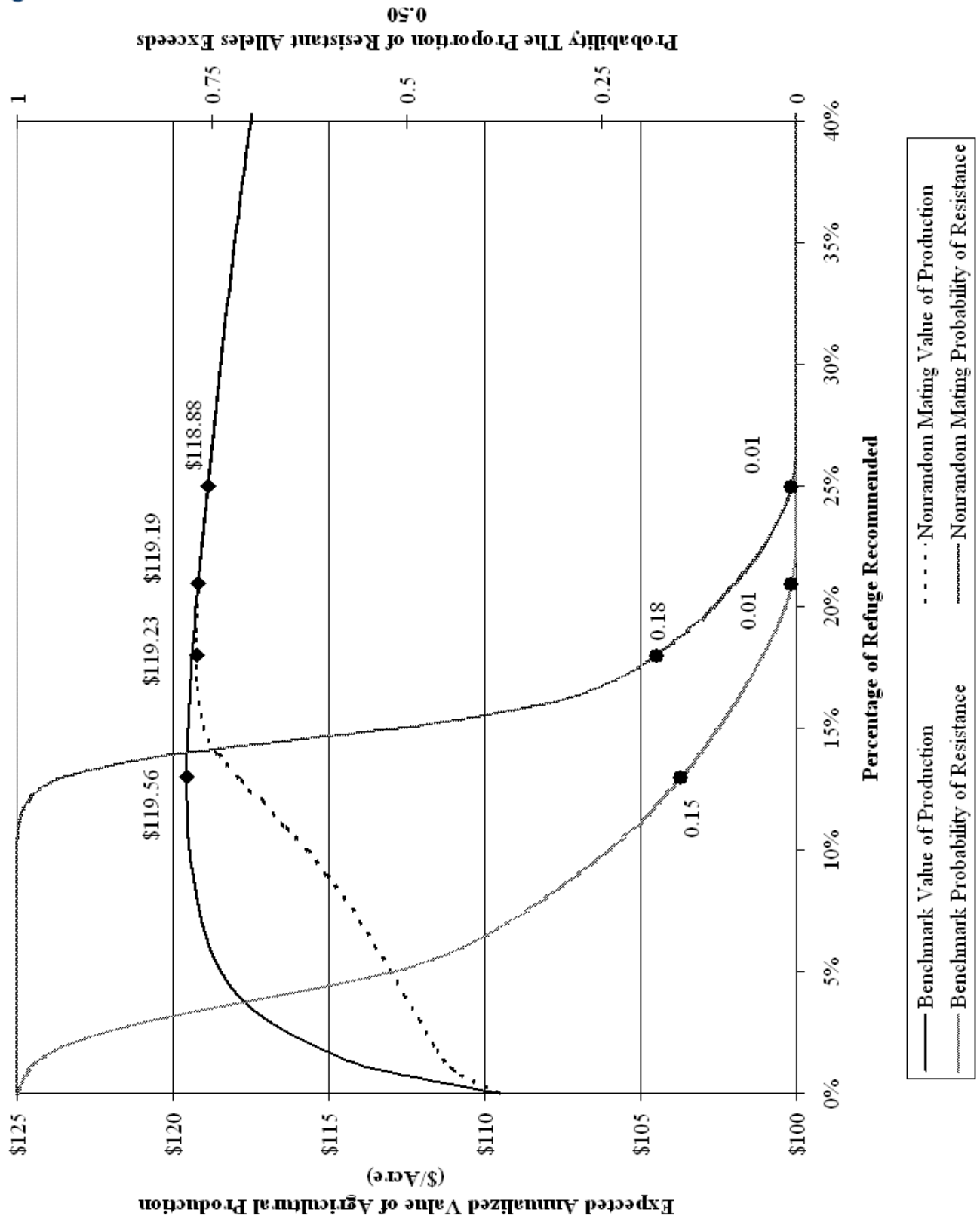




Figure 5.



## Conclusion

The EPA has addressed concerns for ECB resistance to Bt corn by using conditional registrations to provide time for industry to develop effective resistance management plans. The EPA also has supported collaborative efforts among industry, scientists, and producers to build consensus recommendations. The result of this collaborative effort is the identification of the high-dose refuge strategy as an effective means of managing resistance. For a high dose, Bt corn is engineered to express a high enough level of toxin to kill all but the most resistant ECB. For refuge, producers plant acreage in corn where Bt toxins are not used to control the ECB. Unfortunately, consensus has not fully arisen due to disagreement over the appropriate size of refuge necessary to manage resistance.

We have explored four reasons for the failure to reach a consensus: (a) the value of reducing the risk of resistance, (b) the potential introduction of new multiple toxin plants, (c) producer compliance, and (d) the degree of nonrandom mating. Our model shows that refuge recommendations must be made in light of the trade-off between the risk of resistance and the value of agricultural production. We also find that new multiple toxin plants will reduce the need for refuge and that it may be reasonable to lower refuge recommendations if these new plants replace single toxin plants within 10 years. Producer noncompliance may dictate a higher recommendation for the rate of noncompliance that we explore. Finally, we show how differences in the degree of nonrandom mating effect refuge recommendations. When nonrandom mating reduces the effectiveness of refuge, a higher recommendation is appropriate. New information on the degree of random mating in ECB populations has thus created a new issue of contention over the appropriate refuge recommendation.

The degree of nonrandom mating in ECB populations and the degree of producer compliance are two issues that will require additional research to resolve. The value of reducing risk and the appropriate treatment of uncertain technological innovation are two issues that can not be resolved with additional research because they ultimately depend on the stakeholders' judgements of the importance of the risk of resistance relative to the value of increased agricultural productivity. Because industry and producers currently bear the financial cost of reducing the risk of resistance with higher refuge recommendations, they are willing to accept greater risk. Therefore, consensus will remain fleeting unless new ways are found to reduce the cost to producers and industry of reducing the risk of resistance.

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## ENDNOTES

1. These transgenics operate by producing a crystal-like protein (Cry protein) that is a stomach poison for the insect (Ostlie *et al.*, 1997). So far, more than 60 of these proteins have been identified, but the six transgenics registered for commercial use in 1997 utilize only three of them: Cry III A, Cry I(A)b, and Cry I(A)c.
2. The model can easily be extended to address more varied production regions with multiple crops (for instance, corn and cotton) and/or pests (for instance, the ECB and corn ear worm or southwestern corn borer).
3. Dr. Don Alstad and Dr. Dave Andow at the University of Minnesota recently completed a study of the genetic variation in European corn borer populations across the United States. Using ECB collected from sampling sites that were 300 kilometers apart, they find significant population structuring that indicates minimal immigration between sampling location. The data indicates that the reasonable size of a production region is probably less than 300 kilometers.
4. The EPA registers events for pesticidal GMOs. An event consists of the active pesticidal ingredient and the genetic material necessary for the expression of that ingredient.
5. Of the four events registered for corn in time for the 1997 growing season, all relied on either the Cry I(A)b or Cry I(A)c proteins. Since these two proteins have similar modes of action, strong cross-resistance is expected, which would make the toxins virtually identical from a resistance management perspective. Another important difference in these events is the degree to which they express the Cry I proteins throughout the growing season. Incomplete expression of Cry I proteins throughout the growing season has important implications for resistance management that are addressed by Onstad and Gould (1998b).
6. The Hardy-Weinberg principle is a very general model that lies at the foundation of population genetics because of its remarkable ability to predict gene frequencies. The fundamental assumptions of the Hardy-Weinberg principle are (i) the pest is a diploid, (ii) reproduction is sexual, (iii) generations do not overlap, (iv) mating is random, (v) the population is large, (vi) migration is negligible, (vii) mutation is negligible, and (viii) selection is negligible (Hartl, 1988). As with previous studies, we assume the resistant gene is not sex linked. Assumptions (i)-(iii) and (v) are generally satisfied for ECB populations, (iv) is a source of controversy, (vi) and (vii) are assumed, and (viii) is explicitly accounted for by the model.
7. The importance of the independence assumption can not be overemphasized. Without independence, multiple toxin events will behave similarly to single toxin events, which greatly diminishes the resistance management benefits of multiple toxins. Here independence can fail if the genes are linked. A linkage parameter has been incorporated into the model. We will not explore the effect of this linkage because it is currently not an important source of controversy.
8. Even if the genes conferring resistance are independent, there could be other environmental factors that result in correlated survival rate. Since correlation in survival rates due to environmental factors is currently not an important point of controversy, we choose not to further complicate the analysis.
9. Personal communication with Dr. David Andow and Dr. Donald Alstad at the University of Minnesota.
10. Peferoen (1997) finds that resistance may confer a fitness cost, in which case our assumption is conservative.
11. Depending on the rate of adoption of Bt corn, there could be the supply-side price effects. These price effects could depend on refuge size, if there is significant refuge acreage. However, until more is known about the potential adoption rates and changes in the supply of corn, we maintain the assumption of a constant real price of corn.

12. Although industry uses various quality control measures, inevitably some Bt corn plants fail to express Bt. Monsanto attempts to insure that less than 4 percent of Bt plants fail to express Bt (personal communication with Dr. Paula Davis from Monsanto).
13. The expected annualized value of agricultural production and the probability of resistance are calculated using Monte Carlo methods with ten thousand draws.

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